THE PHYLOGENY OF THE ANGIOSPERMS

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The gist of this paper was presented at a symposium of the Western Society of Naturalists, honoring Dr. Douglas H. Campbell, at Monterey, California, December 21, 1939. The title is that of one of Dr. Campbell's papers (6). I owe it to Dr. Campbell to make it clear that some of the opinions stated are not his.

The concept of phylogeny is in modern biology intimately bound up with that of natural classification; and the natural classification of the flowering plants is, and has been for some three hundred years, one of the major problems of science. The history of work on this problem may be represented by a phylogenetic tree, which, by a figure of speech, may be called a phylogeny of phylogenies (text fig. 1, a)

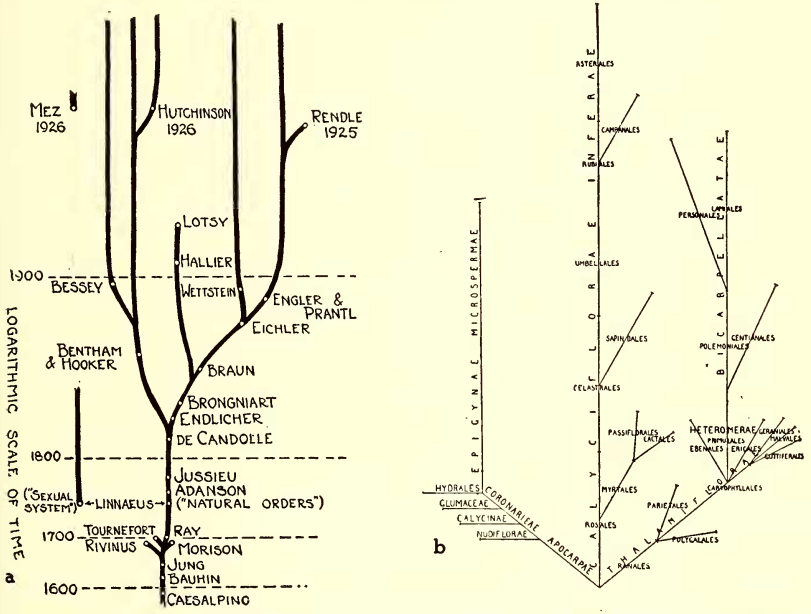

FIG. 1. Phylogenetic diagrams: *a*, "phylogeny of phylogenies"; *b*, phylogeny of the angiosperms according to Bessey, Bot. Gaz. 24: 177. 1897.

The earlier names in this history are now merely of historical interest. It may be worth while, as a matter of historical accuracy and justice, to justify the position of Linnaeus in the main line of development of the natural system. It is generally known that he appended to his Genera Plantarum (21) a list of fifty-eight natural orders, not described, but identified by lists of included genera. It is noteworthy that in this list he recognized

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the distinction, discovered by Ray, between monocots and dicots; though he does not use the names of these groups. In effect, he did what we do in any modern manual: he prefixed an acknowledgedly artificial key to an attemptedly natural arrangement of the genera. It is not he, but the smaller men who followed him, who may be said to have delayed the development of the natural system by an uncritical acceptance of his artificial system. It is further to be noted that Adanson (1), to whom a place in the history of natural classification is generally conceded, set up a series of families exactly as many as the natural orders of Linnaeus, many of them being the same groups.

Botanists of the early nineteenth century referred to the "natural orders of Jussieu" as if to imply that Jussieu had founded natural orders, or even the natural system. More justly, we would attribute to Jussieu the popularization of the idea of natural orders. He made the recognition of natural orders a practical convenience by the establishment of a system of named higher groups to include them. The skeleton of his system is as follows (19):

I. Acotyledones, i. e., seedless plants: Class I.
II. Monocotyledones
    Stamina hypogyna: Class II.
    Stamina perigyna: Class III.
    Stamina epigyna: Class IV.
III. Dicotyledones
    Apetalae
        Stamina epigyna: Class V.
        Stamina perigyna: Class VI.
        Stamina hypogyna: Class VII.
    Monopetalae
        Stamina hypogyna: Class VIII.
        Stamina perigyna: Class IX.
        Stamina epigyna, antheris connatis: Class X.
        Stamina epigyna, antheris liberis: Class XI.
    Polypetalae
        Stamina epigyna: Class XII.
        Stamina hypogyna: Class XIII.
        Stamina perigyna: Class XIV.
    Diclines irregulares: Class XV; orders Euphorbiae, Cucurbitaceae, Urticeae, Amentaceae, and Coniferae.

It was not arbitrarily, but according to precedent, that Jussieu treated the category of classes as of rather low rank, and that he designated the classes by number rather than by name. The varying sequence of the hypogynous, perigynous, and epigynous subdivisions was evidently intended to prôvide transitions linking together the series of main groups respectively of monocots, apetalae, monopetalae, and polypetalae. These groups as

main groups of angiosperms, and their subdivision primarily by hypogyny, perigyny, or epigyny, have to a considerable extent remained in use through the hundred and fifty years to the present time. The sequence in which these groups are arranged has, however, been changed repeatedly.

During most of the nineteenth century, the ideas of the de Candolles were dominant. The original Candollean arrangement need not be presented. The fundamental difference between gymnosperms and proper dicots having been pointed out by Robert Brown, the following modification of the Candollean system was put forward by Asa Gray (15):

Series I. Phaenogamous or flowering plants.
Class I. Dicotyledons.
Subclass I. Angiosperms.
Div. 1. Polypetalous.
Div. 2. Gamopetalous (Monopetalous).
Div. 3. Apetalous.
Subclass II. Gymnosperms.
Class II. Monocotyledons.
Series II. Cryptogamous or flowerless plants.

The sequence just quoted was followed by Bentham and Hooker (3) in what has turned out to be the ultimate elaboration of the Candollean system.

In the mean time the classification of angiosperms had undergone in Germany an independent development. This culminated in the system of Engler and Prantl (10), summarized as follows:

Seedless plants.
Gymnosperms.
Monocots.
Apetalae.
Choripetalae (i. e., Polypetalae).
Sympetalae (i. e., Monopetalae or Gamopetalae).

This system was explicitly an attempt to represent phylogeny. Engler was highly conscious of the prevalence of parallel evolution. He supposed that various groups of Apetalae and Choripetalae, as well as the whole group of monocots, had originated independently of one another from a hypothetical extinct group of gymnosperms; and that various groups of sympetalae had had an independent origin among the Choripetalae. The Apetalae, Choripetalae, and Sympetalae, then, are to be regarded not as natural groups but as evolutionary levels. The system was presented to the world in an extensive work, useful in the recognition and placing of all the genera, written in a modern language, profusely illustrated, and supported by the prestige of the German science of the time. It was generally accepted as the true system; most herbaria and most manuals follow it.

The status of the Englerian system as the accepted system has for half a century made it a prime object of attack. The principle of the representation of phylogeny is universally accepted; but whereas Engler used this principle to justify the resurrection of features of the system of Jussieu, those who have refused to follow him have tended to use it to justify features of the Candollean system. Three systems which exhibit this tendency are now to be discussed.

1. Bessey (4) put forward a system represented by the phylogenetic tree here reproduced (text fig. 1, b). He assumes that the whole group of angiosperms, and its two main subdivisions, monocots and dicots, are natural groups; that among dicots the Choripetalae, and particularly the order Ranales, are primitive and a natural group; but that Apetalae and Sympetalae are not natural groups, each including more than one line of descent from Choripetalae. He drops all three as taxonomic groups: he arranges the orders of dicots in two series, distinguished by hypogyny on the one hand as contrasted with perigyny or epigyny on the other. In effect, he makes a primary division by the character which Jussieu had used in making a secondary division. It is an obvious criticism, that perigyny and epigyny cannot be assumed to be the marks of a single evolutionary line: surely, these characters have appeared repeatedly, just as have apetaly and sympetaly. The Besseyan system has never commanded wide acceptance, but it must be regarded as a living system, having been followed in recent works by Clements and Clements (8), Pool (23), and Swingle (25).

2. Hallier (16), like Bessey, regarded Angiospermae, Monocotyledoneae, and Dicotyledoneae as natural groups, and Ranales as primitive; but his system does not resemble that of Bessey in detail. He supposed Sterculiaceae to be an important secondary center of variation derived from Ranales. He was followed by Lotsy (22) in a work which was never completed. He has had few other followers; he wasted his energies to an unseemly extent in railing against *"Engler und seine geistigen Kinder und Enkel"* (17).

3. Hutchinson (18), like Bessey and Hallier, postulates the naturalness of Angiospermae, Monocotyledoneae, and Dicotyledoneae, and the primitiveness of Ranales. The distinguishing feature of his system is the emphasis placed upon growth form, that is, on the woody as contrasted with the herbaceous character. Woodiness is assumed to be primitive, and the herbaceous dicots are for the most part arranged in a single derived line of descent. This arrangement is open to essentially the same criticism as that of Bessey, in that it assumes a certain evolutionary change to have taken place only once, when it may well have taken place many times. I do not know that this system has been followed in any manuals or herbaria; but it is a living

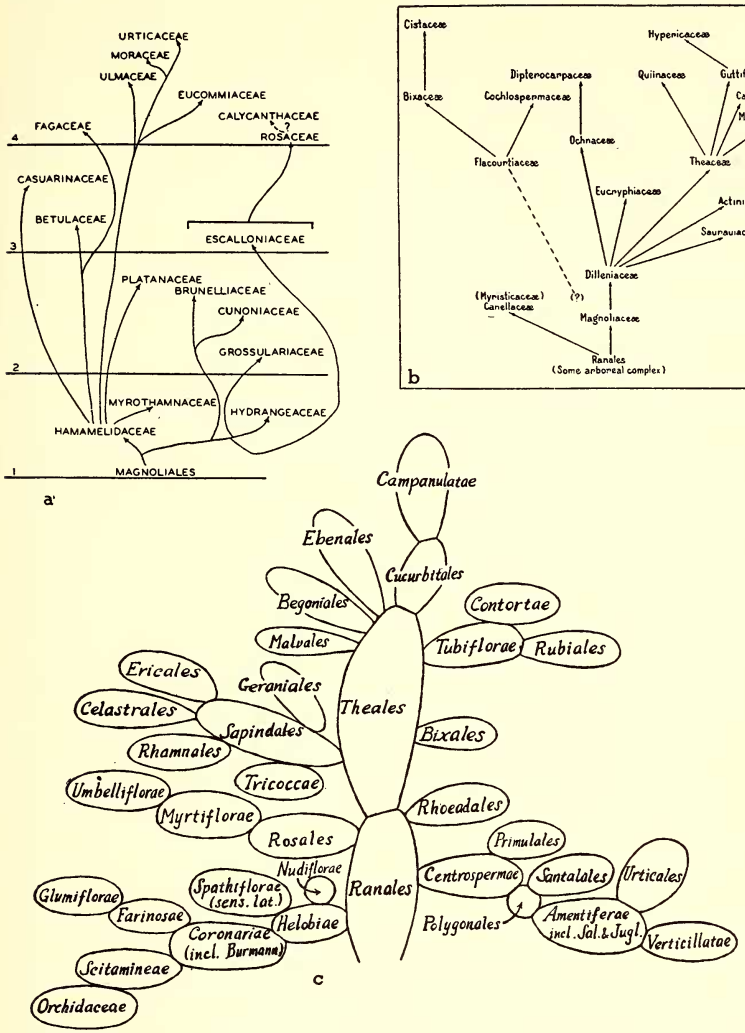

FIG. 2. Phylogenetic diagrams: *a*, phylogeny of Urticales and related groups according to Tippo; *b*, phylogeny of Theineae according to Vestal; *c*, the orders of angiosperms (as limited by various authorities) arranged according to Mez.

system in the sense that it demands consideration whenever the relationships of any family are under discussion.

The history just sketched is that of a persistent effort to divide the dicots into a small number of easily distinguishable natural groups. The effort has been a failure; one or more of the subdivisions established by each system have turned out to be products of parallel evolution. The characters used have been matters of gross morphology. The leaders of botany, the framers of systems, have not been unaware of the necessity of

considering all characters. They have used gross characters because these were known, being easily recognizable in dried specimens and recorded for the whole range of higher plants. When the Englerian system appeared, no phase of the anatomical, chemical, or physiological branches of botany afforded a body of data adequate for taxonomic application. More recently, several such bodies of data have accumulated to the extent that their significance can be estimated; four of these are now to be discussed.

1. The leader in the study of the vascular anatomy of the receptacle has been Eames (9), and the center of study has been Cornell. It has been found that in Magnoliaceae and Ranunculaceae the vascular supply of the floral parts is essentially that of vegetative leaves. Fusion or suppression of floral leaves is accompanied—or preceded or followed—by fusion or suppression in the vascular system: the cauline nature of the receptacle, and the foliar nature of the other parts of the flower, may become unrecognizable. It is evident from this body of data that the Ranales are primitive and that there has been much parallel evolution.

2. The main outline of the embryogeny of angiosperms was worked out by Hofmeister. Early comparative studies gave the impression that the group is quite uniform. When, therefore, Treub (28) discovered chalazogamy and other abnormalities in *Casuarina,* he concluded that this genus should be placed in a class by itself, distinct from both monocots and dicots. Again, when Campbell (5) discovered in *Peperomia* an embryo sac which does not at all conform to the normal type, he concluded that Piperaceae is an ancient group, of distinct origin from the angiosperms with normal embryo sacs. In short, the period when the embryogeny of angiosperms was supposed to be quite uniform was followed by one in which it was supposed to be so varied as to indicate multiple origin. Some forty more years have passed; Chicago and Vienna have been centers of embryological study, and Schnarf (24) has prepared a useful compendium of the results up to 1930. It is found that the type of embryo sac which includes eight nuclei derived from one which is produced by reduction division is indeed the normal type. It occurs in the overwhelming majority of the families; it extends to groups as far apart as Ranales, Campanulatae, and Glumiflorae. From the normal type there are parallel deviations which result, for example, in the same derived type in families as far apart as Liliaceae and Plumbaginaceae. In the order Myrtiflorae, most of the families exhibit the normal type; Onagraceae has a peculiar type of its own; Penaeaceae and the genus *Gunnera* have developed the same peculiarities as *Peperomia.* Characters of the embryo sac, then, decidedly make it probable that the angiosperms are a natural group. The normal type embryo sac is primitive, and deviations from it indicate derivation; but it sur-

vives in groups otherwise highly advanced. In the several other embryological characters, various features are marks of natural groups: thus a developing endosperm which consists of four cells in a row marks the order Ericales.

3. The comparative anatomy of woods has been studied notably at Harvard. There has been developed a doctrine of the evolution of vessels (11, 12, 13); of wood rays (20); and of wood parenchyma. The anatomy of wood is held not in itself to indicate natural groups, but only degree of evolution; it is used to test hypotheses that this group is derived from that, and yields as answer either "it is possible" or "it is impossible." The effect has been to demonstrate the parallel evolution of many lines of woody plants from a common source in or near Magnoliaceae. Herbaceous plants are interpreted as having originated repeatedly in primitively woody groups. Some of the detailed results may be presented. Tippo (27) finds it probable that Fagaceae and Betulaceae, Urticales, and *Casuarina* are closely related (text fig. 2, a) all being descended through Hamamelidaceae from Magnoliaceae. Juglandaceae and Aristolochiaceae, which fall near these families in the Englerian system, are found to have nothing to do with them. Vestal (29) has worked out the phylogeny (text fig. 2, b) of the group called Theineae in the Englerian system. He finds it a primitive group, connected directly with Magnoliaceae. The group which Hutchinson calls Bixales is not closely allied with it. This group Theineae or Theales or Guttiferales is of particular interest to me because I believe that both Ericales and Ebenales are derived from it—Ericales from Saurauiaceae, Ebenales from Theaceae.

4. Tests for immunity—"serum diagnosis" or "immune reactions"—were first used for the identification for certain diseases and the bacteria which cause them. An animal, being rendered immune by vaccination to a certain organism, reacts in various ways, by agglutination, precipitation, or anaphylaxis, when exposed to protein of the species to which it is immune. It shows the same reactions in lower degree to proteins of related species. These immune reactions are characteristic of proteins in general, not only of those of bacteria. The study of reactions to plant proteins has been carried out chiefly by Mez, of Königsberg. The work has been reviewed in English by Chester (7). In 1926 it had been carried so far as to yield a complete phylogenetic tree. According to Chester, the pictorial representation published at that time is protected by copyright and cannot be reproduced; it is available in the work of Gortner (14). I have constructed from the original tree of families a tree of orders (text fig. 2, c). Some of the features of this tree are surprising: our authorities on wood anatomy would not allow the derivation of Amentiferae from Centrospermae, nor the inclusion of Juglandaceae in Amentiferae, nor the derivation of Bixales from Theales; and for my own part I am not content with the position

of Ericales. Theoretically the method is sound; I would conclude that it has not been adequately calibrated, that the degree to which conclusions can be drawn from the direct results has not been established. With an engine of the power of this one at our disposal, we are not wise in failing to use it when hypotheses as to relationship are to be tested. It is to be remarked that the use of the method is arduous and exacting, and quite outside of the range of technique in which botanical taxonomists are trained.

Apologies may here be offered, in that several other bodies of pertinent data—ecology, chemical characters aside from immune reactions, details of the structure of pollen grains, cytology and genetics—are not discussed. I am not aware that a science of systematic physiology has so much as been conceived; but physiological data are susceptible of systematic treatment. In the long run, these thing will have to be taken into account.

Meanwhile, the four bodies of data discussed are conspicuously in agreement with each other and with the views of Bessey, Hallier, and Hutchinson, in making the Angiospermae a natural group and the Ranales primitive. These points should, I think, be accepted as positively established. If the Ranales are primitive, the angiosperms are not descended from the specialized group of Gnetineae; nor from the cycadeoids (Wieland, 30), in which the carpels are reduced to stalks bearing solitary ovules; nor from the Caytoniales (Thomas, 26), in which the ovules are enclosed by the incurving ends of blades. No known plant, living or fossil, has the sort of carpel we require of the ancestors of the angiosperms, except only the genus *Cycas*; and in features other than the carpels, *Cycas* is not a good match for the hypothetical progenitor of the group. We are forced to postulate as such some extinct group of Cycadineae. This is the conclusion reached long ago by Arber and Parkin (2).

From the Ranales the other angiosperms are derived, either directly or through secondary centers of variation, one of which appears to be Theales. They fall into many lines of descent. One such line, derived directly from Ranales, is the whole group of monocots; these are bound together not only by monocotyledony but by the whole range of their characters. Others are in general yet to be worked out. It is not probable that any of them will be found at the same time so extensive and so well marked as the monocots. Some or many of them may be definable by definite characters, as is the group of monocots. On the other hand, in view of the prevalence of parallel evolution, we should accustom ourselves to the probable necessity of accepting named taxonomic groups like the natural orders of Linnaeus, definable only by the list of groups included. Already it seems probable that the line of apetalous trees culminating in *Casuarina* should be accepted as constituting the order Amentiferae: but it is not easy to frame a list of characters by which it will include

Hamamelidaceae and Platanaceae while excluding Salicaceae and Juglandaceae.

When a group is assigned to its true place, it becomes inextricable: every character studied increases the certainty of the assignment. Many current hypotheses as to location show signs of becoming stronger; many families are letting it be known that their true place has been discovered. Not merely within the lifetime of contemporary taxonomists, but within a decade or two, there should be few families left to be placed by guess, as being too isolated by evolution, or too poorly known, for definite location.

Demonstration of the true phylogeny of all or of nearly all angiosperms will result automatically in revision of the taxonomic system; but it will not determine the names, nor the precise limits, nor in all cases the sequence, of the groups which are to be accepted. One is tempted to discuss features which may make one taxonomic arrangement preferable to another: but they are matters of taste or of mere accident. We may expect presently the establishment of a more sound and more stable taxonomic system than we have ever had, being a solution, as to the main outlines, of the long-standing problem of the classification of flowering plants.

Sacramento Junior College,
Sacramento, California,
February 3, 1940.

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STUDIES IN WESTERN VIOLETS—III

Milo S. Baker

The investigation of certain problems concerning the violets of the Pacific Northwest called for field study; to this end during the month of June, 1938 and 1939, trips were taken through western Oregon, Washington and British Columbia to visit the localities in which the problems centered.

Viola ocellata Torr. & Gray. Through correspondence with Mrs. Cora Ollivant I had learned that *Viola ocellata* had been collected in the vicinity of Looking Glass Post Office, a few miles southwest of Roseburg, Oregon, on the ranch of Thomas Ollivant. This is a matter of interest to students of *Viola* since this species was not known with certainty to grow in Oregon, its most northern known limits being northern Humboldt County and central Shasta County in California. In Gray's "Synoptical Flora," published in 1897, it was stated that this violet had been collected in the Cow Creek Mountains of Oregon, but diligent inquiry on my part had until now failed to confirm this report. On a hillside at a distance of less than a mile from the ranch house there was a colony of this violet. Although not covering a wide area here, the colony was flourishing and the individuals appeared very similar to typical California plants. Both transplants and herba-